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AUTHOR(S):

UEDA, HIROSHI

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# Mechanisms of salmon homing migration from molecules to behavior

HIROSHI UEDA

*Laboratory of Aquatic Ecosystem Conservation*

*Field Science Center for Northern Biosphere*

*Hokkaido University*

*Sapporo, 060-0809 Hokkaido, Japan*

*hueda@fsc.hokudai.ac.jp*

## ABSTRACT

A number of studies have investigated the amazing ability of salmon to migrate long distances from the ocean to their natal river for spawning. For a better understanding of the mechanisms of salmon homing migration, three different analyses have recently been applied using Japanese chum salmon (*Oncorhynchus keta*). The first is behavioral analysis using electromyogram (EMG) transmitters to monitor chum salmon upstream migration in the Shibetsu River where the restoration of river environments by reconstruction of meanders was carried out in Japan. The second is endocrinological analysis on two molecular types of gonadotropin-releasing hormone (GnRH: salmon GnRH and chicken II GnRH) profiles in the various brain regions of chum salmon during spawning migration using specific time-resolved fluoroimmunoassay systems. The third is olfactory discriminating analysis on upstream selective movement of chum salmon in a two-choice test tank using artificial home stream water that was prepared based on the compositions of amino acids and related substances of their natal river. This paper will provide a new concept for the mechanisms of homing migration in salmon from molecules to behavior.

**KEYWORDS:** Homing migration, behavior, hormone, olfaction, chum salmon

## INTRODUCTION

Salmon have an amazing ability to migrate thousands kilometers from the open ocean to their natal stream for reproduction after several years of oceanic feeding migration. It is now widely accepted that some specific factors of the natal stream are imprinted to particular nervous systems of juvenile salmon during downstream migration, and that adult salmon evoke these factors to recognize the natal stream during homing migration (Fig. 1). A number of studies have investigated the amazing ability of salmon to migrate long distances from the ocean to their natal river for spawning (Ueda and Shoji, 2002). For a better understanding on the mechanisms of salmon homing migration, three different analyses have recently been applied using Japanese chum salmon (*Oncorhynchus keta*) migrating from the Bering Sea to Japan and then to their natal river.

### Behavioral analysis

The first is behavioral analysis on swimming speeds of homing chum salmon by means of a micro-data logger having a propeller (Tanaka et al., 2005). Swimming speeds in the oceanic phase can be one of the keys to understand the mechanism of chum salmon homing migration. We tagged a maturing chum salmon (fork length = 685 mm) which was considered to be of Japanese origin with

a data logger (sampling intervals: speed and depth = 5 sec; temperature = 60 sec) in the central Bering Sea on July 9, 2000. This salmon was retrieved by a set net along the eastern Hokkaido coast 67 days after the release, and 51-day data were recorded. The fish usually swam in the surface water column and rarely stayed deeper than 50 m. The average swimming speed was 60–70 cm per sec, and horizontal rate calculated by an empirical relationship between the attack angle and vertical rate was 42.3–47.7 km per day. The estimated horizontal rate indicates that chum salmon traveled 2,763 km in 67 days, which is almost equivalent to the distance between points of release and retrieve. It implies that chum salmon moved to the coastal area near the spawning ground almost straightly from the Bering Sea. All through the recording period, chum salmon showed a clear foraging period in the daytime, which consisted of repeated short diving from the surface water column to the depth beyond the thermocline. It indicates that chum salmon traveled searching a prey patch during their oceanic migration. These results suggest that homing chum salmon migrated along the continental shelf of Kuril Islands.

Another behavioral analysis on upstream tactics of chum salmon through a rehabilitated segment of the Shibetsu River by electromyogram (EMG) telemetry and micro-data logger (Akita et

al., 2005). To restore the ecological condition of a previously channelized river to its more natural, meandering state, a segment of the Shibetsu River was reconstructed. We investigated the upstream tactics of chum salmon as they migrated up the channelized segment, reached the confluence point with the restructured segment, and then entered the rehabilitated area. Fish were radio tracked with EMG telemetry and micro-data loggers. The monitored salmon preferred to hold in deep, slow moving areas of the channelized river, and EMG telemetry data revealed that these extended holding times provided the fish with efficient rest. In the reconstructed segment, the fish swam at more shallow depths and against stronger currents. Although all fish chose to enter the reconstructed segment, few fish remained in the segment for long. This implies that the reconstructed area may not provide suitable holding sites for migrating salmon.

### Endocrinological analysis

The second is endocrinological analysis on hormone profiles in the brain-pituitary-gonadal axis (Fig. 2). Gonadotropin-releasing hormone molecules produced in the various brain regions are considered to be involved in many physiological functions of teleost life cycle. In order to clarify GnRH roles on salmon homing migration, measurements of two molecular types of GnRH, salmon GnRH (sGnRH) and chicken GnRH-II (cGnRH-II) in different brain regions, as well as gonadotropin (GTH) and steroid hormones were conducted using specific time-resolved fluoroimmunoassay (TR-FIA) systems (Yamada et al., 2002; Leonard et al., 2002). Maturing chum salmon were caught in nine points from the Bering Sea to the Chitose River. After decapitation, the brain was divided into six regions; olfactory bulb (OB), telencephalon (TC), diencephalon (DC), optic tectum (OT), cerebellum (CB), and medulla oblongata (MO). During spawning migration of chum salmon, sGnRH levels in OB, TC, and pituitary of both sexes were increased at the coastal sea to the branch point of the Chitose River from the Ishikari River. Moreover, sGnRH levels in the pituitary tended to increase at the same time of elevation in female pituitary GTH II and ovarian GTH I levels. cGnRH-II level in MO was increased at the pre-spawning ground in both sexes, and levels of OT were also increased in males (Kitani et al., 2003). Both GnRH levels in DC showed no significant changes during spawning migration. GTH II levels in gonads were not detected though the sampling period. Serum steroid hormone levels showed similar profiles as previous observations (Ueda 1999); estradiol-17 $\beta$  in females and 11-ketotestosterone in males increased during vitellogenesis and

spermatogenesis, respectively, and 17 $\alpha$ ,20 $\beta$ -dihydroxy-4-pregnen-3-one increased dramatically at the time of final gonadal maturation in both sexes. It is quite interesting to note that both sGnRH content in TC and serum testosterone level showed coincident peaks at the branch point of the Chitose River from the Ishikari River. These results confirm the previous findings that sGnRH plays a role on GTH secretion in the pituitary of chum salmon, and sGnRH and cGnRH-II might be involved in brain region-dependent roles on sexual maturation and behavior in salmonid fishes.

### Olfactory analysis

The third is olfactory analysis on discriminating ability of the natal river. For upstream homing migration from the coastal area to the natal stream, the olfactory hypothesis proposed by Hasler and Wisby (1951) has been discussed in many behavioral and electrophysiological studies, but the odor substances of home stream are still unknown. We found that the response to artificial stream water based on the compositions of amino acids and salts closely resembled the response to the corresponding natural water (Shoji et al., 2000), and we carried out behavior experiments to test whether amino acids mixtures of the home stream have attractive effects on chum salmon upstream movement. Mature male chum salmon (mainly 4 year olds) were captured at the weir in the Osaru River, Hokkaido, Japan, in the late spawning season of 2002, transferred to the Toya Lake Station, Hokkaido University, and reared for several days before experiments. Behavior experiments were conducted in the two-choice test tank. The artificial home stream water was prepared by the amino acid and related substance composition of the Osaru River and dissolved in artificial freshwater. A total of 44 chum salmon was tested, and 28 fish (63.6%) showed upstream movement to one of the choice arm. Among those that moved, 24 fish (85.7%) were found in the arm running the artificial home stream water, and 4 fish (14.3%) were observed in the arm running the natural lake water (Fig. 3). These results demonstrate clearly that the artificial home stream water reconstituted by the amino acid composition of home stream has attractive effects on the chum salmon upstream selective movement. We concluded that amino acids dissolved in the home stream water are home stream odorants, and the hypothesis that amino acids dissolved in stream waters are home stream substances for salmon homing is strongly supported by these results.

### Future researches

By means of these different new approaches, the following three topics will be future research

projects on chum salmon homing migration from the Bering Sea to Japan in my laboratory.

- 1) What kinds of environmental factors might influence on endocrinological changes of salmon, which will initiate homing migration ?
- 2) When, where, and why might salmon cease foraging behavior during homing migration ?
- 3) What kinds of sensory cues might salmon use to navigate for several thousands kilometer migration, and how endocrinological changes would influence on sensory cues during homing migration ?

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#### Figure legends

Fig. 1. Life history of two different types of Pacific salmon in Japan. Dotted line:

chum and pink salmon; Solid line: sockeye and masu salmon.

Fig. 2. Brain-pituitary-gonadal axis in salmon.

Fig. 3. Selectivity of stream water by mature male chum salmon in two-choice water arm. The number in parenthesis indicates fish moved to each stream water.